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THE RELATIONSHIP BETWEEN BURROW ABUNDANCE AND AREA AS A PREDICTOR OF GOPHER TORTOISE POPULATION SIZE

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ABSTRACT: Because gopher tortoises (Gopherus polyphemus) occupy high-value lands in the southeastern United States, are declining throughout their range, and stir public passion when they are entombed through currently legal take, refined conservation measures for this species are needed. Of particular interest is a determination of how many individuals constitute a population and what sized areas are required by such populations so that animals currently in harm’s way might be moved to designated reserve areas. We use surveys of burrows of gopher tortoises from a large sample of areas of differing sizes to test for a relaxation of the linear relationship between area and number of burrows expected at the edge of a population of gopher tortoises. For measures of burrow abundance, some of our data are from sites on which estimates were based on transect samples; on other sites, complete counts were made. The relationship between area and abundance was elevated for transect samples compared to similar data from complete counts, indicating that transect data yield inflated counts when extrapolated over large areas. For complete counts, our data indicate a threshold point at which a linear relationship between area and abundance ends and a loss of this relationship for larger areas begins. This threshold point suggests that, on average, populations of gopher tortoises consist of 444 burrows, cover 755 ha, and contain 240 tortoises. These figures describe features of tortoises inhabiting a variety of lands that differ in current management goals and past land-use history. Our results suggest that many current reserve areas for gopher tortoises are likely to be too small. Our results also provide an example of how key conservation variables can be generated for long-lived species.

Key words: Gopher tortoise; Gopherus polyphemus; Population size; Reserve area; Segmented regression

In response to growing public concern over legal take of gopher tortoises (Gopherus polyphemus) in Florida, USA, via entombment in their burrows by developers, Hiaasen (2006) led a newspaper column with the statement that “If your kids asked to bury a small animal alive, you’d be horrified.” These words, among others, brought an unusual sense of urgency to revision of Florida’s management policy for gopher tortoises. This urgency is likely to increase the speed with which gopher tortoises will be required to be moved from harm’s way to reserve areas throughout the range of the species. In order for these efforts to lead to sustainable populations, refined estimates of how many gopher tortoises constitute a population and how much area such populations require will be needed.

One approach to determining population size is based on the relationship between the abundance of individuals of a given species and the area that they inhabit (Smallwood, 1999, 2001). In a study of terrestrial Carnivora, Smallwood (1999) reports that plots of raw abundance versus study area size, without log-transforming the variables, reveal a consistent pattern among species: abundance first increases linearly with area and then reaches a plateau where a relationship between abundance and area can no longer be detected. The point at which this plateau is reached is the threshold that represents the minimum area needed to support a spatially constrained population (Smallwood, 1999, 2001). By extension, the number of individuals in a population also can be determined from examining the threshold. Smallwood (1999) argues that the threshold area emerges because animal populations are spatially distinct from one another and require more area than members of the population can inhabit at any one time. Areas smaller than the threshold area do not support an entire population, but rather some fragment of the population, such as one or more breeding pairs or social groups.
The purpose of our research is to evaluate the applicability of the Smallwood abundance–area analysis to a determination of reserve area requirements for the gopher tortoise, a species of conservation concern in the southeastern United States (Diemer, 1986). Data on minimal reserve size are needed as part of region-wide tortoise management and relocation programs, but scientists have not yet reached a consensus on the area needed to support a sustainable tortoise population. McCoy and Mushinsky (2007) document that published area estimates progressively have increased in size, note how costly underestimation of this variable might be, and provide a novel estimate of area needed for gopher tortoise conservation. Their estimate of area is based on a modification of the Smallwood approach and is associated with an expectation that density of animals will increase in small patches of poor but acceptable habitat where animals concentrate due to habitat loss or deterioration in surrounding areas. The point at which density no longer decreases as area increases is the presumed minimum area of a population because this is the point at which area–abundance relationships reach the plateau described by Smallwood (2001). McCoy and Mushinsky (2007) note that this represents an estimate of area needs given modified habitats in the current landscape and recognize a need for similar analyses based on Smallwood’s original evaluation of broader landscapes where animals might distribute themselves in ways that are similar to the ancestral landscape. Here, we present such an analysis, evaluate how differences in sampling methods may influence abundance estimates, and compare our results to other published estimates of reserve area requirements for gopher tortoises (Cox et al., 1987; Eubanks et al., 2002; McCoy and Mushinsky, 2007).

**Materials and Methods**

**Study Species and Sites**

The gopher tortoise inhabits the upland Coastal Plains region of the southeastern United States and its distribution is closely associated with that of the longleaf pine (*Pinus palustris*) vegetation community (Auffenberg and Franz, 1982). In the years following European settlement, over 98% of longleaf pine forests have been destroyed by human activities (Noss, 1989; Simberloff, 1993; Ware et al., 1993); this loss of forest has contributed to a similar decline in gopher tortoise population numbers (Auffenberg and Franz, 1982; Hermann et al., 2002). Additional factors, including fire suppression, poaching, illegal collection, and urban development, have also contributed to gopher tortoise population declines (Diemer, 1986; Landers and Speake, 1980; McCoy et al., 2006). Currently, the gopher tortoise is included either on federal or state lists as a threatened species throughout its range (Diemer, 1986).

Gopher tortoises excavate burrows, which are inhabited year-round, in sandy soils. These burrows can be readily located and identified based on the size and shape of the entrance and the mound of cleared soil (apron) placed in front of the burrow during excavation and maintenance (Auffenberg and Franz, 1982; Guyer and Hermann, 1997; McCoy and Mushinsky, 1992). Most social and feeding activities occur in close proximity to the burrow (Boglioli et al., 2003; McRae et al., 1981) and individual tortoises will use one or more burrows in a single season (Diemer, 1992; Eubanks et al., 2003; McRae et al., 1981; Smith et al., 1997; Wilson et al., 1994). By counting the number of active burrows in a given area, a repeatable estimate of tortoise population size can be generated (Auffenberg and Franz, 1982; Eubanks et al., 2002; McCoy and Mushinsky, 1992), although the exact conversion of burrows to tortoises varies substantially (Breininger et al., 1991; Burke, 1989). Nevertheless, a survey of burrows is the standard method for evaluating areas of conservation concern for gopher tortoises and for delimiting populations of this species.

We conducted comprehensive surveys of tortoise burrows present at 21 study sites in Alabama, Georgia, and Mississippi, USA (Table 1). Only active and recently used burrows were included in each survey. As defined by previous investigators, active tortoise burrows were characterized by an unobstructed entrance shaped like a tortoise carapace and a smoothed apron in front of the burrow entrance, often showing footprints and
tracks left by the plastron of a tortoise (active category, Guyer and Hermann, 1997; active plus inactive categories, Auffenberg and Franz, 1982; Mushinsky and McCoy, 1994). At sites other than Ft. Benning, we located burrows by haphazard searches until no further burrows were discovered within or around the periphery of the study area. During a full season of activity (May through September) all resident tortoises on four sites (Table 1) were captured, affixed with a radio-transmitter, and released (following Eubanks et al., 2003). We then recorded the locations of these individuals 3–5 times per wk. The few burrows that were occupied by telemetered tortoises but had not been previously discovered were added to the inventory of burrows for those sites. We marked all burrow locations with a numbered metal tag staked into the ground near the burrow entrance and recorded latitude and longitude coordinates as measured by a Trimble Global Positioning System (submeter accuracy). We determined the area of each study site by calculating the minimum convex polygon circumscribed by the set of burrow coordinates for a site.

At Ft. Benning, we used data for burrow surveys conducted within each of 52 military training compartments. For each survey, two to four surveyors systematically walked parallel lines spaced 5.0 m apart across the entire compartment and recorded all burrows encountered. This method was similar to surveys done on other federal lands and was designed to assure discovery of all burrows. The activity status of each burrow was recorded, as were latitude and longitude coordinates (as described above). For the purpose of this study, we grouped neighboring compartments into 12 large study areas that were bounded by distinct geographical features (e.g., roads, streams, and buildings) representing barriers to tortoise dispersal. We used natural geographical features rather than compartment boundaries to designate study areas at Ft. Benning because this approach was similar to how the boundaries of our other study sites were chosen and provided areas of much larger size than could be generated at other sites.

We obtained additional values of burrow abundance at sites distributed throughout the gopher tortoise’s range (n = 61 sites; AL: Eubanks et al., 2002; FL: Kushlan and Mazzotti, 1984; McCoy et al., 2002; GA: Boglioli et al., 2000; Hermann et al., 2002; MS: Mann, 1993; SC: Tuberville and Dorcas, 2001). To be included in our analyses, both the abundance of active and recently used burrows and area of the study site must have

<table>
<thead>
<tr>
<th>Location</th>
<th>State</th>
<th>Yr</th>
<th>Burrow no.</th>
<th>Area (ha)</th>
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<td>1997</td>
<td>42</td>
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<td>AL</td>
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<td>2002</td>
<td>134</td>
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<td>1997</td>
<td>8</td>
<td>2.4</td>
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<tr>
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<tr>
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<td>2000</td>
<td>155</td>
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* Tortoises at this site were tracked by radiotelemetry.
been stated or easily calculated from the data provided. The number of burrows on a given study site was surveyed in one of two different ways. In some studies, burrow abundance was obtained by a comprehensive survey of the study area, as we have described for our own study sites. Other studies relied on transect surveys to sample the number of burrows in a given area. For these surveys, fixed-area transects were placed in some subset of the overall study plot. All burrows found within the boundaries of these transects were counted, converted to density, and extrapolated for the entire area of the study site (see McCoy et al., 2002, for additional description of the transect-survey method).

Data Analysis

We first assessed whether survey method influenced the relationship between number of burrows and area of the study site by performing an analysis of covariance (Proc GLM, class = survey method; SAS Institute, 2001). Secondly, we followed the protocol outlined by Smallwood (1999) to examine the relationship between number of burrows and area surveyed. We plotted burrow abundance versus area, without log-transforming the variables, and then systematically removed the sites with the largest abundance values and replotted the abundance–area relationship of the remaining sites. For each plot, we assessed whether the relationship between burrow abundance and area was linear (Proc GLM; SAS Institute, 2001). Following Smallwood’s methodology (1999), both abundance and area values were natural-log–transformed for these regression analyses to meet the assumption of normal distribution of residuals. Finally, we developed a segmented regression model (Proc NLIN; SAS Institute, 2001) to determine whether the slope of the relationship between burrow abundance and area changed at a threshold point. Statistical tests were considered significant at $P < 0.05$.

Results

Overall, tortoise burrow abundance increased significantly with area surveyed ($R^2 = 0.890$, df = 81, $P < 0.0001$). The method by which burrows were surveyed, however, influenced these estimates of burrow abundance. Sites surveyed by a comprehensive count of all burrows contained significantly fewer burrows per unit area than did sites surveyed by line-transects (Fig. 1; $F_{1,82} = 12.1$, $P = 0.0008$). The magnitude of this difference in burrow abundance between the two survey methods was greatest for large study areas, resulting in a statistically significant interaction between area and survey method ($F_{1,82} = 7.1$, $P = 0.009$).

Because the relationship between burrow abundance and area was not independent from survey method, we analyzed the data generated from transect and comprehensive surveys separately. A visual inspection of the plot of burrow number versus area of sites surveyed by line-transects indicated that burrow abundance continued to increase linearly with area and never reached a plateau as predicted by Smallwood (Fig. 2A; $R^2 = 0.818$, df = 27, $P < 0.0001$). As we restricted the number of sites included in this regression analysis by systematically removing those sites with the largest abundance values, the linear relationship between burrow abundance and area...
area persisted (Table 2). In contrast, a visual inspection of the plot of burrow number versus area of sites surveyed by a comprehensive count of tortoise burrows indicated that a threshold was reached at approximately 350 ha, a value above which burrow abundance no longer increased linearly with area (Fig. 2B). The overall regression slope, however, did indicate that the relationship between burrow abundance and area was linear ($R^2 = 0.715$, df = 53, $P < 0.0001$). As with the transect survey data, this linear relationship persisted after sites with the largest abundance values were systematically removed from the analysis (Table 2). The relationship between abundance and area was not linear, however, when only those sites with an area greater than the visually estimated threshold (350 ha) were considered ($R^2 = 0.007$, df = 10, $P = 0.811$).

Our segmented regression analysis revealed that, among sites surveyed by a comprehensive count of all burrows, a threshold point occurred at 755.1 ha (95% CI = 222.2–2566.2 ha), indicating a change from a positive linear slope to a slope that was indistinguishable from zero (Fig. 1B). This plateau occurred when the population size equaled 444 burrows, or approximately 240 tortoises (burrow-to-tortoise correction factor = 0.54, Nomani et al., 2008). In contrast, we did not detect a threshold point in our analysis of sites surveyed by line-transects.

**DISCUSSION**

Our results indicate that an assessment of the burrow abundance of gopher tortoises is biased by survey method. Abundance estimates obtained from transect surveys were greater per unit area relative to estimates obtained from comprehensive surveys. Furthermore, the overall relationship between burrow abundance and area was incongruent for the two survey methods. Burrow abundance estimated by transect surveys increased linearly with area; in contrast, abundance estimated by comprehensive surveys increased with area at smaller sites but was independent from area at larger sites. We conclude that the differences between the two methods results from biased placement or insufficient replication of transects. Although both types of surveys typically are conducted in places where tortoises are known or suspected to be present, transects commonly are used to sample large areas where comprehensive surveys are difficult. In such samples, transect data often are extrapolated over much larger areas that may include...
habitats unoccupied by tortoises (Hermann et al., 2002). Particularly at extremely large sites, the actual area included in the transect lines can be very small relative to the entire area of the site (e.g., Mushinsky and McCoy, 1994), increasing the likelihood that abundance estimates are inflated relative to the number of burrows actually present. We did not control for any geographical difference in tortoise density, which also may explain the difference in burrow abundance estimates between the survey types. Most of the sites surveyed by line-transects were located in Florida, where gopher tortoise density is reported to be greater than in the northern portions of its range (Auffenberg and Franz, 1982). Direct comparisons of survey method on burrow abundance estimates within the same site, however, have shown that transect surveys can overestimate burrow abundance (Mann, 1993), suggesting that methodological rather than geographical factors influenced our results. This is not say that transect methods are without value. When implemented with appropriate statistical rigor (total transect length sufficiently long to achieve an acceptable coefficient of variation; transects uniformly distributed across sample area) this method can achieve values of burrow density that are comparable to comprehensive counts (Nomani et al., 2008). Apparently, these statistical considerations, on average, were not part of the studies from which we drew examples.

When only comprehensive surveys of burrow abundance are considered, the relationship between abundance and area fits the pattern described by Smallwood (1999, 2001) for other vertebrate species. The segmented regression model that we developed identified a threshold area that was twice as large as that predicted by a simple visual inspection of the abundance–area plot (755 ha versus 350 ha), although the range of values included in the 95% confidence interval was large. Interestingly, only four sites surveyed by transect lines were larger than this threshold area; all of these sites also were larger than any site surveyed by a comprehensive count of burrows. Thus, we may have lacked a spectrum of areas broad enough to allow us to identify a plateau in the abundance–area relationship for sites surveyed by transect lines. The four largest sites may instead represent a larger scale domain of abundance (see Smallwood, 1999), such as a metapopulation, rather than a single population of gopher tortoises. Transect surveys of sites in the 744–6000-ha size range are needed to evaluate this alternative. However, the effort required to achieve the sampling protocols outlined in Nomani et al. (2008) are daunting on sites of this size.

If the threshold area identified in this study represents the minimum area needed to support a population of gopher tortoises distributed broadly across current landscapes, then the areas required for tortoise conservation will need to be revised upward considerably. The modification of the Smallwood method implemented by McCoy and Mushinsky (2007) indicates that areas on the order of 140–150 ha will be required to maintain populations of gopher tortoises; our implementation of the full Smallwood method increases this by a factor of about 5. Both of these estimates are substantially larger than the estimates of 10–20 ha of Cox et al. (1987) and of 25–81 ha of Eubanks et al. (2002). However, the areas used in our study do not share management goals or past land-use histories. Therefore, they do not represent how gopher tortoises are likely to perform in areas that mimic the ancestral landscape. Instead, the varied management goals and land-use histories are likely to have reduced tortoise abundances relative to what might be achieved if the lands were all managed with frequent fire and contained the uneven-aged trees of old-growth longleaf pine forests (Hermann et al., 2002). Therefore, we are in agreement with McCoy and Mushinsky (2007) that conservation of gopher tortoises likely can be realized on reserves that are smaller than our estimates, but only if significant efforts are made to manage the lands more aggressively than is the current norm for such lands.

Although both Cox et al. (1987) and Eubanks et al. (2002) assumed a population of 50 adult tortoises to be sustainable, no data exist to support this assumption. McCoy and Mushinsky (2007) estimate that their minimum conservation areas will contain 110–310 tortoises and our estimate (240 tortoises) for burrows across a broader landscape is in
accord with these numbers. The two studies are also in accord that these tortoises will occupy between 400 (this study) and 500 (McCoy and Mushinsky, 2007) burrows. Again, these estimates increase substantially the values that should be used in conservation planning to describe what constitutes a population of gopher tortoises.

Despite its protected status, the gopher tortoise remains a species of conservation concern, as evidenced by a recent study showing that tortoise abundance has declined at 8 out of 10 protected sites in Florida over the past 20 yr (McCoy et al., 2006). Notably, the largest Florida area sampled (599 ha) was smaller than the threshold area that our analysis indicates is needed to support a tortoise population. In fact, only 15% of the sites included in our study are large enough to meet this criterion. Therefore, like McCoy et al. (2006), we are concerned that the sizes of many current protected sites harboring gopher tortoises are too small to assure persistence of this keynote species of longleaf pine forest ecosystems.

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